

# THE MORPHOLOGY AND SHELL MICROSTRUCTURE OF THE THECIDEIDINE BRACHIOPOD *ANCORELLINA AGERI* FROM THE LOWER JURASSIC OF ARGENTINA

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**ABSTRACT.** Serial sectioning of complete shells of *Ancorellina ageri* enables the first description of dorsal valve internal morphology and shell microstructure. The diagnostic description by Manceñido and Damborenea (1990) is inadequate, as the supposedly diagnostic features of the *Ancorellina* hemispondylium are known to occur in the Aalenian thecidellinid *Moorellina*. However, the *Ancorellina* brachidium, consisting of a laterally supported bifurcating column, is currently unique in the Thecideidina. The early ontogeny conforms with the thecideid pattern. The adult brachidium is believed to have supported a ptychoploche and may be interpreted as a precursor of the ramulate condition of lacazellins. Accordingly, the genus is placed in a new subfamily, *Ancorellinae*, in the family Thecideidae. The brachidium-supporting pillars resemble the hamate skeletal structures of thecospirellids, introducing the possibility that thecospirellids are close to thecideid ancestral stock. The shell microstructure indicates a phylogenetic link with the Carnian *Thecospira haidingeri* and probable dispersal from Tethyan faunas early in the Early Jurassic.

THE first Lower Jurassic thecideidine brachiopod from South America was reported by Manceñido and Damborenea (1990), and was known only from complete shells and separated ventral valves occurring as cryptically cementing epifauna on anthozoan and oyster substrates. Features of the interior of the dorsal valve remained unknown, although, viewed externally, traces of structure visible through the shell suggested a monoseptate condition. The authors did not present a formal systematic diagnosis of *Ancorellina* because of the essentially palaeobiological/palaeogeographical content of their contribution. Subsequently, serial sectioning has revealed the presence of an unusual brachial skeleton in the genus and a formal diagnosis is now presented.

## MATERIAL AND METHODS

Specimens of *Ancorellina ageri* were detached from their substrate (underside of scleractinian corals) and prepared using the techniques documented by Baker and Elston (1984, p. 777).

*Registration of material.* The syntypes (MLP12197, 18289–18290, 24470) together with original and duplicate acetate peels of the serially sectioned hypotypes (PB3257–3258) figured in this paper are housed in La Plata Natural Sciences Museum, Argentina.

## SYSTEMATIC PALAEONTOLOGY

Order SPIRIFERIDA Waagen, 1883

Suborder THECIDEIDINA Elliott, 1958

Superfamily THECIDEOIDEA Gray, 1840

Family THECIDEIDAE Gray, 1840

Subfamily ANCORELLININAE subfam. nov.

*Diagnosis.* Forms with median septum resorbed posteriorly; brachidium consisting of an anterior, distally bifurcated median column supported by a pair of anterolaterally placed pillars and directed posteroventrally; lophophore probably ptycholophous; fibrous secondary shell continuous in both valves.

*Age.* Early Jurassic.

## Genus ANCORELLINA Manceñido and Damborenea, 1990

*Derivation of name.* From the Latin *ancora*, after its peculiar anchor-shaped structure.

*Type species.* *Ancorellina ageri* Manceñido and Damborenea, 1990.

*Age.* Early Jurassic, Late Pliensbachian.

*Diagnosis.* Ancorellinin with relatively large cicatrix and well-developed free ventral wall; ventral interarea reduced; pseudodeltidium indistinct; hinge line short; ventral valve with sessile hemispondylium raised anteriorly to form spoon-like termination; dorsal valve with relatively massive cardinal process and median septum reduced to anteroposteriorly flattened, distally bifurcated column, each limb united laterally with pillar arising from anterior of each brachial cavity; endopunctate.

*Ancorellina ageri* Manceñido and Damborenea, 1990

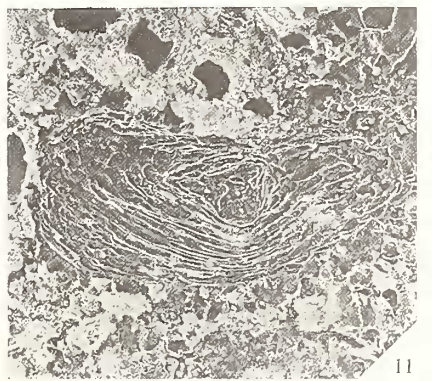
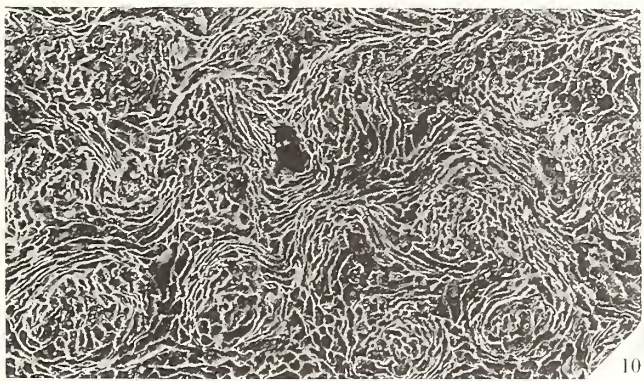
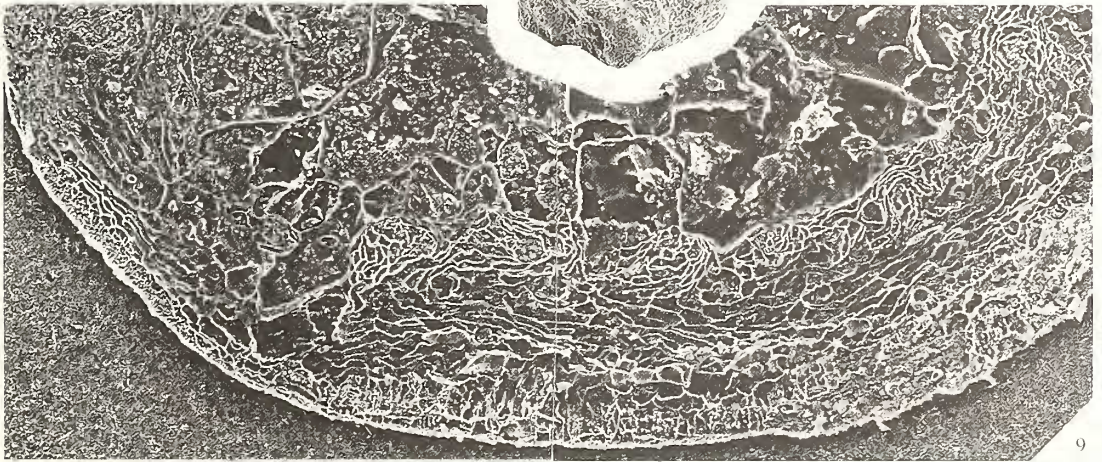
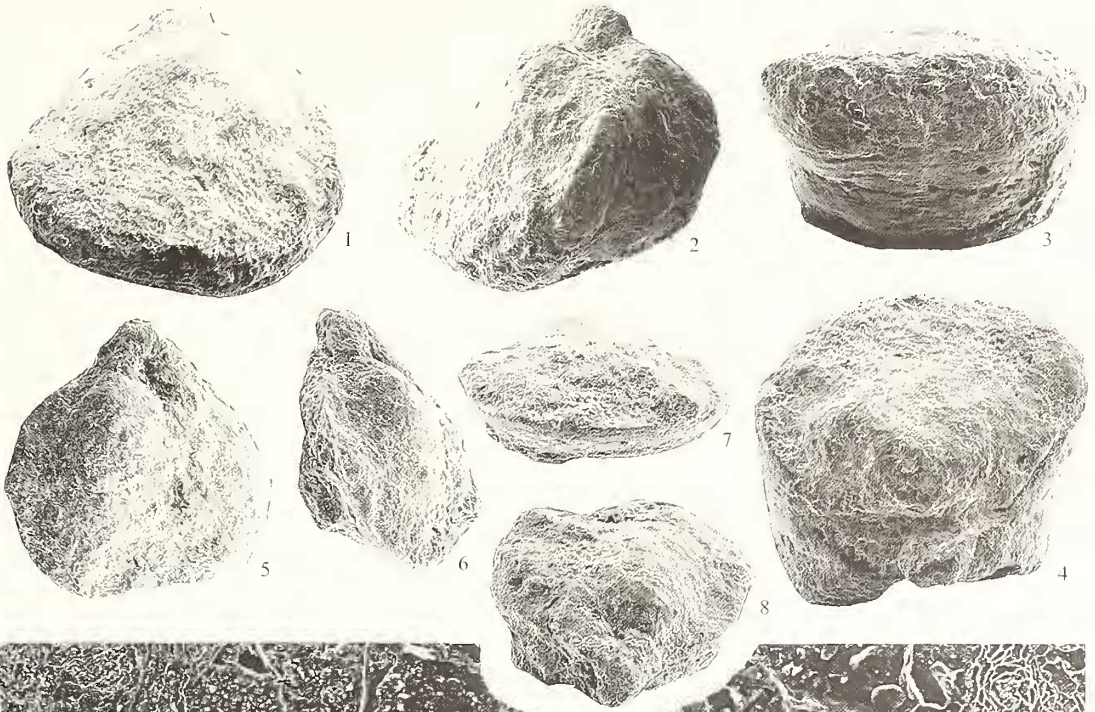
Plates 1–2; Text-figures 1–3

1990 *Ancorellina ageri* Manceñido and Damborenea, p. 90, fig. 1.

## EXPLANATION OF PLATE I

Figs 1–11. *Ancorellina ageri* Manceñido and Damborenea, 1990. Upper Pliensbachian; Neuquén, Argentina. 1–4, PB3257; dorsal, lateral, anterior and posterior views, photographic record of hypotype, sectioned adult shell; the apparent ventral umbo is shown by sectioning to be an adherent matrix artefact;  $\times 20$ . 5–8, PB3258; dorsal, lateral, anterior and posterior views, photographic record of hypotype, sectioned presumed juvenile shell;  $\times 44$ . 9, PB3258/8; near transverse section through the ventral valve free ventral wall; showing the granular primary layer (extreme left) and fibrous secondary layer with the early development of tubercles (inner boundary) (section orientation as in Text-fig. 2);  $\times 240$ . 10, PB3257/42; dorsal valve; showing the 'chaotic' disturbance of the fibrous secondary shell layer resulting from close spacing of tubercles (section orientation as in Text-fig. 1; section location, right anterolateral sector);  $\times 240$ . 11, PB3257/32; near transverse section through the dorsal median column showing the oblique secondary fibre orientation;  $\times 225$ .

All scanning electron micrographs of gold-coated material; figures 9–11 are of cellulose acetate peels of sectioned specimens.



*Type specimens.* Holotype not designated; species erected on syntypes MLP12197, MLP18289–18290, MLP24470; hypotypes PB3257–3258.

*Emended diagnosis.* *Ancorellina* up to about 2.5 mm long, 3.0 mm wide and 1.5 mm thick; sub-circular in outline, commonly with incipient anterior sulcus; pseudodeltidium barely demarcated; hinge line short, about half maximum width of shell; dorsal umbo quite prominent but with no trace of dorsal interarea, valve rather flattened away from umbonal region; endopunctae with restricted distribution.

*Description.* A small thecideid, sub-circular in outline, with a relatively large attachment scar and well-developed free ventral wall, commonly with incipient sulcus, giving a ventribiconvex lateral profile. The ventral interarea is small with an indistinct pseudodeltidium. The overall weak convexity of the dorsal valve is masked by the prominent development of the umbonal region. Endopunctuation possibly confined to the dorsal valve.

*Distribution.* Currently known only from the Piedra Pintada area, Neuquén, Argentina. The material was collected from strata of Late Pliensbachian age (*Fanninoceras* ammonite Zone, *Radulonecites sosneadoensis* bivalve Assemblage Zone (Riccardi *et al.* 1989)).

## MORPHOLOGY, GROWTH AND SHELL MICROSTRUCTURE

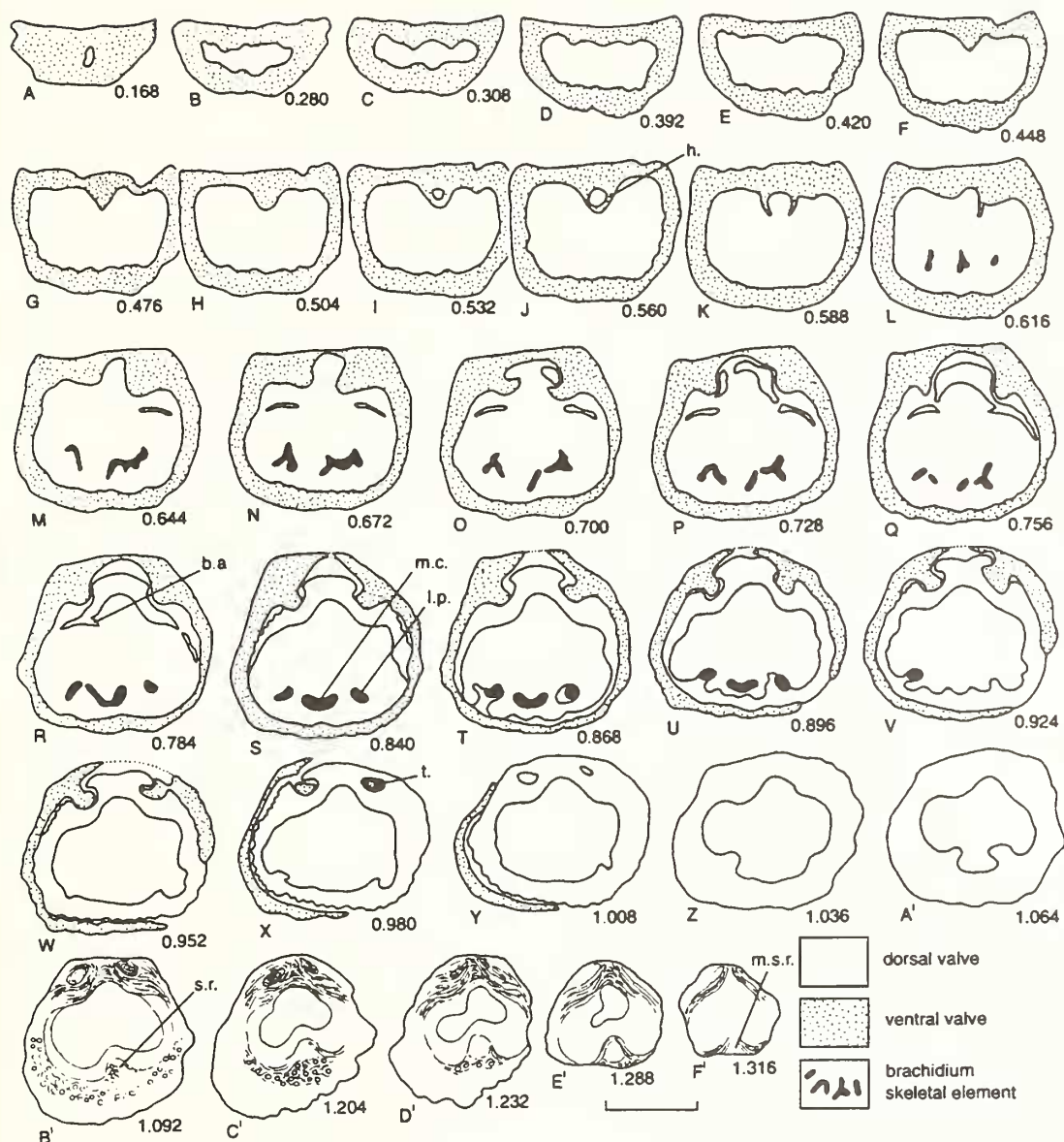
### *Valve characters*

*Ventral valve* (Text-figs 1A–Y, 2A–G). The pseudodeltidium is not demarcated externally but its presence is marked by a delthyrial notch flanked by well-developed, boss-like, cyrtomatodont teeth.

Although the anterior is raised (Pl. 2, fig. 2), the posterior of the sessile hemispondylium is sunk into the floor of the valve between thickened dental ridges. Anterior to the hemispondylium, a median ridge extends as far as the base of the free ventral wall, dividing the body cavity overlying the area of attachment into two large shallow oval depressions. The valve peripheral margin is ornamented by tubercles.

*Dorsal valve* (Text-figs 1L–F', 2F–J, 3A–D). The cardinal process is relatively large and incipiently trilobed, and the inner socket ridges are strongly developed although the bridge abutments are small. The subperipheral rim is narrow and ornamented by one or two rows of tubercles. The posterior of the median septum is resorbed and the anterior is extended posteroventrally as an anteroposteriorly flattened column about 0.5 mm wide and 0.4 mm high, bifurcated for about half its length. The brachial cavities are devoid of brachial lobes but, from the anterior of each, a pillar about 0.2 mm thick rises to unite with the distal bifurcation of the median column. The shell is penetrated by irregularly distributed endopunctae (Pl. 2, fig. 1).

*Ontogeny.* The ontogeny of *A. ageri* has been deduced partly from serial sections of a juvenile shell and partly from the preservation of ontogenetic relics buried in adult shell fabric. Although the scarcity of material makes it difficult to be certain, the free ventral wall just beginning to grow away from the substrate, associated with the cicatrix occupying most of the ventral valve surface, and the relatively prominent dorsal umbo of specimen PB3528 (Pl. 1, fig. 7), are characteristic of other thecideidines known to be juvenile specimens (Nekvasilová 1967; Baker 1989). The shell microstructure (Pl. 1, fig. 9) is essentially the same as that of the adult specimen (PB3527). Therefore, on the basis of morphology and shell microstructure, specimen PB3528 is assumed to be a juvenile *A. ageri*. Horizontal sections show that in the ventral valve (Text-fig. 2D–E), the robust dental ridges are an early development, but the characteristic hemispondylium and median ridge appear later. Horizontal sections through the dorsal valve (Text-fig. 2F–J), reveal the presence of a short dorsal median septum and no evidence of skeletal brachial supports. Buried ontogenetic relics in the adult shell fabric (Pl. 2, fig. 1; Text-fig. 1B'–F') suggest that the anterior of the median septum broadened and developed an early sinus typical of the early ontogeny of thecideid genera (Pajaud and Smirnova 1971; Baker and Laurie 1978; Baker and Elston 1984).



TEXT-FIG. 1. *Ancorellina ageri* Manceño and Damborenea, 1960. A-F', 'Wild' stereomicroscope traces of cellulose acetate peels (out of series 1-50) of serial sections through specimen PB3257. Plane of section horizontal, approximately parallel with the commissural plane. Gross shell fabric mosaic included in dorsal valve traces B'-F', clearly indicating the ontogenetic relic of a broad median septum with sinus. Abbreviations: b.a., bridge abutment; h., hemispondylium; l.p., lateral pillar; m.c., median column; m.s.r., juvenile median septum relic; s.r., juvenile median sinus relic; t., hinge tooth. Numbers indicate peel cumulative distance in mm from base of free ventral wall (as seen in Pl. 1, fig. 3). Scale bar represents 1 mm.

*Microstructure.* In common with other Lower Jurassic thecideidines, fibrous secondary shell forms a continuous lining in both valves. Because of exfoliation loss, the granular primary shell layer (Pl. 2, fig. 4) is of indeterminate thickness in the specimens studied but the preservation of growth line

traces (Pl. 1, fig. 3) suggests that it must have been thin, possibly *c.* 25  $\mu\text{m}$  thick. In the well-preserved fibrous secondary shell, fibres are deflected around closely spaced (rarely > 20  $\mu\text{m}$  apart) fibrous tubercle cores 30–40  $\mu\text{m}$  in diameter. The close spacing of the tubercles, and consequent distortion of the fibrous secondary shell lining associated with them, produces a characteristically 'chaotic' gross fabric (Pl. 1, fig. 10). In the ventral valve, the tubercle cores are orientated almost parallel with the shell surface and, in anterolateral sectors, the disturbed mosaic associated with them forms an inner layer separated from the primary shell by an outer layer of tubercle-free, more uniformly arranged fibres with a length orientation almost at right angles to those of the inner layer (Pl. 2, fig. 3). In the dorsal valve, the tubercle cores are almost perpendicular to the shell surface and the disruption of the fibrous secondary shell affects the whole shell layer (Pl. 1, fig. 10). The brachial skeleton is also composed of fibrous shell (Pl. 1, fig. 11) with the fibres apparently obliquely spiralled relative to the median column and pillar axes. Endopunctae have only been recognized in lateral and posterolateral sectors of the dorsal valve. The ventral valve is apparently impunctate.

## DISCUSSION

### *Morphology*

In *Ancorellina*, the form of the hemispondylium with its raised anterior termination (anchor-like structure of Manceñido and Damborenea 1990) is unusual, and the posterior depression into the floor of the ventral valve suggests that the diductor muscle scars were impressed as in *Pachymoorellina* (Baker 1989). The resorbed median septum succeeded by the 'three-pronged' brachidium is reminiscent of an attempt at a perforate *Lacazella*-like ramulate skeletal support so that, although no trace of lophophore grooves was detected, the configuration of the brachial skeleton suggests that the lophophore was in the form of a ptychophe. The weakly developed crura were possibly not united to form a bridge.

### *Microstructure*

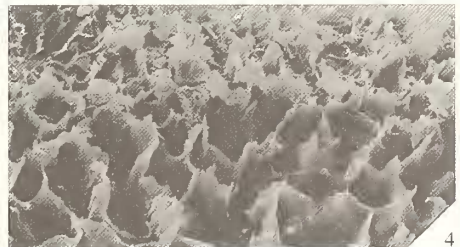
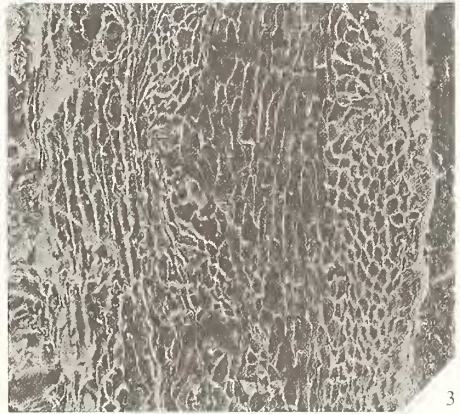
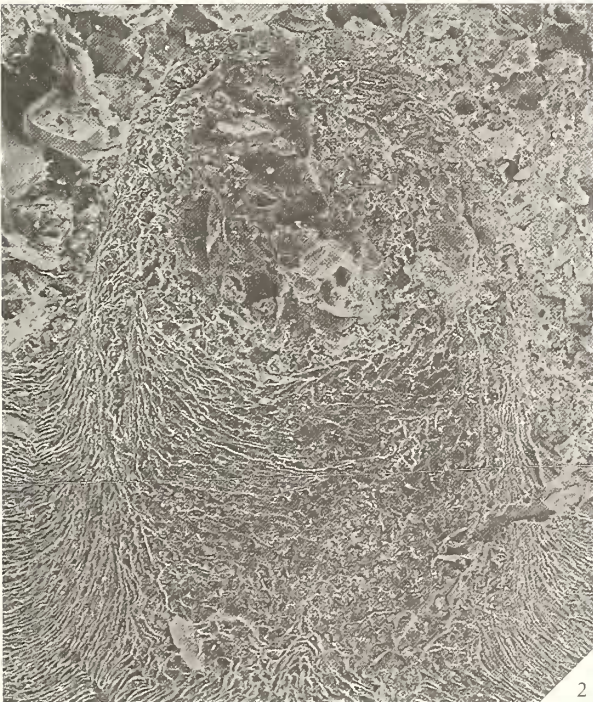
The fibrous secondary shell gross mosaic is similar to that described in the Aalenian thecidellinid *Moorellina* Elliott, 1953 (Baker 1970). Although the fibrous tubercle cores and 'laminar layering' typical of the *Moorellina* free ventral wall (Baker 1970, p. 88) are seen in *Ancorellina*, in the latter genus the tubercles are not reniform in transverse section. Similarly in the dorsal valve, although the disturbed fibrous secondary mosaic is very similar in both genera, *Moorellina* has granular calcite tubercle cores. Although the diameter of the tubercles (30–40  $\mu\text{m}$ ) is approximately the same, they are much more closely spaced in *Ancorellina* (15–20  $\mu\text{m}$ ; *Moorellina* 20–60  $\mu\text{m}$ ). In *Ancorellina*, the close spacing and consequent 'chaotic' disruption of the secondary mosaic gives a gross fabric almost identical with that of *Thecospira haidingeri* (Suess, 1854) (compare Pl. 1, fig. 10 with Benigni and Ferliga 1989, p. 531, fig. 13).

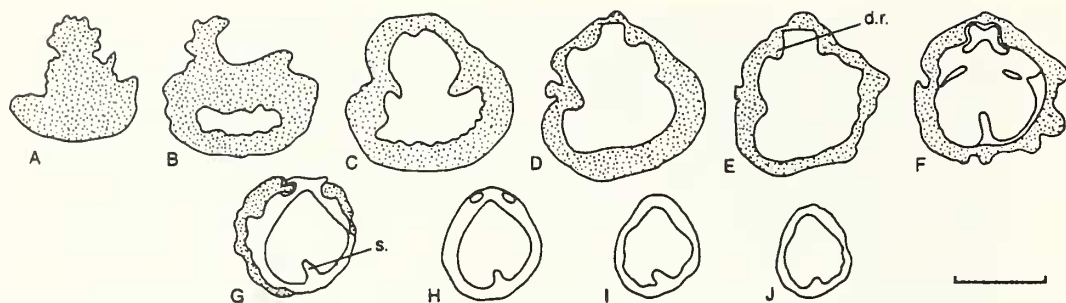
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## EXPLANATION OF PLATE 2

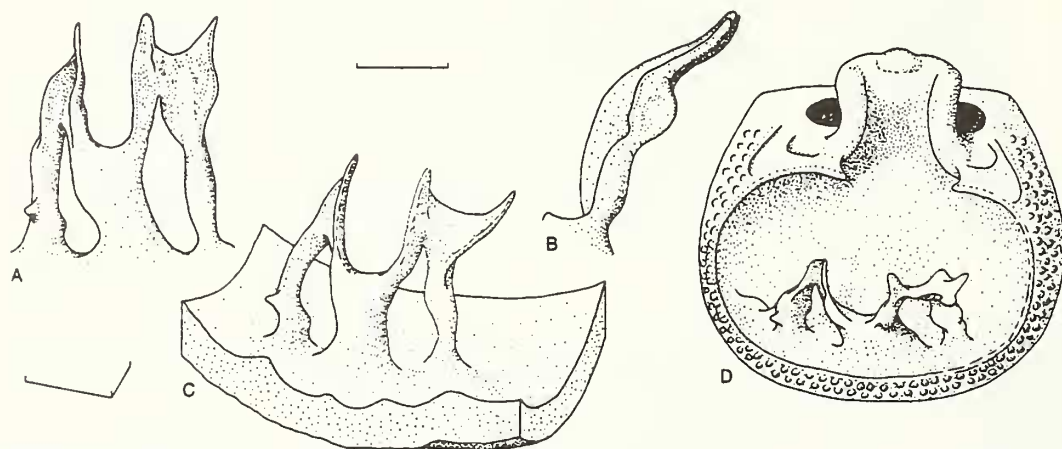
Figs 1–4. *Ancorellina ageri* Manceñido and Damborenea, 1960. 1, PB3257/46; dorsal valve, showing endopunctae and buried ontogenetic relic of juvenile median septum with sinus; the floor of the sinus has been breached through exfoliation loss of outer shell (section orientation as in Text-fig. 1; section location, mid-line approximately 0.8 mm from dorsal umbo);  $\times 240$ . 2–4, PB3257/20; ventral valve. 2, oblique section through the anterior of the hemispondylium, showing the raised spoon-like termination; the apparent perforation is a function of the orientation of the section (as in fig. 1);  $\times 240$ . 3, showing the differing orientation of secondary fibres in the inner and outer regions of the fibrous secondary shell layer of the ventral valve (section location, free ventral wall, anterolateral sector);  $\times 375$ . 4, showing junction between the granular primary and fibrous secondary shell layers (section location as fig. 3);  $\times 1500$ .

All scanning electron micrographs of gold-coated cellulose acetate peels of sectioned specimens.





TEXT-FIG. 2. *Ancorellina ageri* Manceñido and Damborenea, 1960. A–J, 'Wild' stereomicroscope traces of cellulose acetate peels (6–15 out of series 1–15) of serial sections through juvenile specimen PB3258. Plane of section horizontal, relative to the attachment cicatrix; intersecting the commissural plane with an angle of about 5° ventral deflection. Abbreviations: d.r., dental ridge; s., medium septum. Ventral valve stippled. Peel interval approximately 20  $\mu$ m. Scale bar represents 0.5 mm.



TEXT-FIG. 3. *Ancorellina ageri* Manceñido and Damborenea, 1960. A–B, reconstruction of the brachial skeleton of serially sectioned specimen PB3257 based on a vertical plot of the data from acetate peels 20–28 and 30–34 (Text-fig. 1J–W). A, anterior view, and B, lateral view showing the posteroventrally directed distally bifurcated median column and lateral supporting pillars; vertical scale  $\times 3.5$  horizontal. C, skewed 'idealized' compilation of data from figs A and B showing the brachial skeleton of *Ancorellina* in oblique profile. Vertical scale  $\times 3$  horizontal. D, reconstruction of the interior of the dorsal valve of *A. ageri* based on superimposition of data from acetate peels 20–50 inclusive. Scale bars represent 0.5 mm.

### Geographical distribution

Although morphological similarity may be explained by the homoeomorphy likely to be encountered in reef-associated faunas (Baker 1984), the physiological processes involved in the secretion of such a closely similar secondary shell fabric in *Ancorellina* and *Thecospira* must indicate a close phylogenetic relationship. The occurrence of *Ancorellina* in the Pliensbachian of Argentina therefore has interesting palaeogeographical implications. Despite their wide geographical separation, it seems that the Argentinian Pliensbachian thecideids are genetically linked with Tethyan thecospirids of Carnian age, although whether the dispersal of the Tethyan populations was via the Hispanic Corridor (Smith and Tipper 1986) (Central Atlantic Seaway of Manceñido and Damborenea 1990) rather than the circum-Antarctic Australasian migration route around southern Gondwanaland, involving 'island hopping' (Stanley and McRoberts 1993) or teleplanic larval



(Newton 1988) strategies, remains unclear. However, as a cemented representative of cryptic epifauna, the opportunities for large jump larval dispersal must have been limited and, as the central Pacific Ocean was at its widest during the Pliensbachian, the Hispanic Corridor route is probably to be preferred.

### CONCLUSIONS

Although the general shell microstructure shows a thecospirid affinity and the anterolaterally placed pillars possibly equate with the hamate structures (Dagis 1973) of thecospirellids, the evidence of the juvenile median septum with an anterior sinus, succeeded by a crudely ramulate brachidium, suggests that *Ancorellina* is an early thecideid close to the ancestral stock of the *Lacazella* line. It has been generally accepted (Baker 1990) that the hungarithecids are ancestral to the thecideoids and the current study confirms the relationship with thecospiroids. However, the evidence provided by *Ancorellina*, viewed in conjunction with the differing thecideid and thecidellinid early ontogenies (Smirnova 1984), raises the possibility that the two thecideoid stocks diverged early and although the thecidellinids remain close to the hungarithecids, the thecideids may be much closer to the thecospirellids than was formerly thought. If this turns out to be the case, the presence of two clearly differentiated thecideoid lines in the Upper Triassic suggests that the separation of thecospiroids and thecideoids occurred much earlier than is currently believed and that the ancestor of the thecideidines should possibly be sought among reef-associated faunas of Permian age.

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Typescript received 6th December 1995  
Revised typescript received 19 February 1996